

WATER USE STRATEGIES OF FIVE SYMPATRIC SPECIES OF *QUERCUS* IN CENTRAL COASTAL CALIFORNIA

JOHANNES M. H. KNOPS¹

Department of Botany, Arizona State University, Tempe, AZ 85287

WALTER D. KOENIG

Hastings Natural History Reservation, University of California,
38601 E. Carmel Valley Road, Carmel Valley, CA 93924

ABSTRACT

We examined the late summer predawn and midday xylem water potential of 247 trees of five *Quercus* species at the Hastings Reservation in central coastal California. These five species are sympatric over a large part of their range in California, but show markedly different strategies in water acquisition and use. *Quercus douglasii* and *Q. kelloggii*, two deciduous species, had the lowest daytime xylem water potentials and the highest recovery values, indicating considerable drought tolerance. *Quercus lobata*, a third deciduous species, had consistently high predawn values, indicating access to ground water and hence the greatest drought avoidance. The two evergreen species, *Q. agrifolia* and *Q. chrysolepis*, had the lowest recovery values, consistent with shifting part of their growth to the winter as part of a drought evading strategy. Correlations between xylem water potential and tree size (DBH) were positive for *Q. agrifolia* but otherwise weak. Elevational effects were significant for several species but did not consistently correlate with elevational preferences. Topographic correlates of water availability as they are usually envisioned did not predict water stress as indicated by xylem water potential. Water relations help explain the distributional differences of these species. *Quercus lobata* consistently taps the water table on alluvial terraces where the water table is too low for other species, such as *Q. agrifolia*, to reach. *Quercus agrifolia* is able to grow in drier environments than *Q. lobata*. *Quercus chrysolepis* is similar to *Q. agrifolia*. *Quercus douglasii* and *Q. kelloggii* are highly drought tolerant and able to grow in dry soils.

The climate in much of California is characterized by wet winters and dry summers. This pattern severely limits plant growth (Hanes 1965). Plants exhibit three general strategies for dealing with the problems associated with such climates: (1) Drought avoidance—Avoidance of desiccation, for example by improved water uptake, water reservoirs or a reduction of transpiring surfaces (Larcher 1980); (2) Drought tolerance—Physical and physiological modifications allowing plants to tolerate extremely dry conditions; (3) Drought evading—A shift in the growing season to the wetter but colder periods of the year (Larcher 1980).

¹ Present address: Hastings Natural History Reservation, 38601 E. Carmel Valley Road, Carmel Valley, California 93924.

Oaks dominate the vegetation over a large part of California, often with several species occurring sympatrically (Cooper 1922; Griffin 1977; Sawyer et al. 1977). Within a given vegetation type, species are often spatially separated. Several authors have related this to soil water availability. Cooper (1926), for example, remarked that *Q. agrifolia* grows mainly close to streams and has a superficial root system while *Q. lobata* has a well developed tap root, capable of exploiting deep-seated water.

We measured the xylem water potential of 247 trees of five California *Quercus* species at Hastings Reservation in central coastal California with the goal of understanding the adaptations they exhibit to cope with the rigors of a Mediterranean climate and the way that these adaptations allow closely related species to coexist. By measuring xylem water potential in late summer both at predawn, when trees have fully rehydrated, and during the day, when water stress is at its maximum, we made three measurements of water relations: (1) Daytime xylem water potential (DAY)—A low value indicates drought tolerance and ability to cope with dry conditions; (2) Nighttime, predawn xylem water potential (PREDAWN)—A high value indicates that the tree has considerable water resources available to it, most likely by being rooted to deep-seated ground water; (3) Overnight recovery (RECOVERY)—This value is the difference between (2) and (1). A low overnight recovery indicates that rehydration is limited, resulting in lower stomatal conductance (Waring et al. 1981). Because there is a direct relationship between water loss and photosynthesis (Farquhar and Sharkey 1982), photosynthesis is potentially limited by this lack of rehydration. Individuals exhibiting low overnight recovery are most likely shifting part of their growth to other seasons, as has been documented for *Q. agrifolia* relative to *Q. lobata* (Hollinger 1992). Low recovery consequently suggests drought evasion.

STUDY SITE AND METHODS

Study site. The study was conducted at Hastings Natural History Reservation, Monterey County, located in the northern Santa Lucia Mountains of central coastal California (36°23'N, 121°33'W) approximately 20 km east of the Pacific Ocean at an elevation of 500 to 900 m. The climate is Mediterranean with a mean annual rainfall of 540 mm (range 261 to 1112 mm), over 90% of which falls from November to April. The mean minimum temperature varies from 1.4°C in January to 9.7°C in August, the mean maximum from 15.6°C in January to 30.4°C in July.

Hastings Reservation is situated in the middle of the central coast range, which stretches from San Francisco to Santa Barbara. The vegetation consists of a patchwork of chaparral, valley grasslands,

TABLE 1. NAMES AND CHARACTERISTICS OF OAKS USED IN THIS STUDY. Values are for trees sampled at Hastings Reservation and are compared with Kruskal-Wallis 1-way ANOVAs (df = 4); values are means \pm SD (coefficient of variation). Mean aspect excludes trees growing on level slopes; value presented is calculated using circular statistics. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Subgenus	Species						χ^2
	<i>Q. lobata</i>	<i>Q. douglasii</i>	<i>Q. chrysolepis</i>	<i>Q. agrifolia</i>	<i>Q. kelloggii</i>		
Deciduous?	<i>Quercus</i> ("white") Yes	<i>Quercus</i> ("white") Yes	<i>Protobalanus</i> ("intermediate") No	<i>Erythrobalanus</i> ("black") No	<i>Erythrobalanus</i> ("black") Yes		
n trees	87	56	21	63	20		
DBH (cm)	80.6 \pm 33.8	64.2 \pm 24.7	50.8 \pm 27.3	76.2 \pm 29.4	82.0 \pm 36.0		24.0***
Stems	1.05 \pm 0.30	1.04 \pm 0.26	2.57 \pm 2.20	1.29 \pm 0.68	1.00 \pm 0.00		59.4***
Basal area (cm ²)	6069 \pm 4975	3729 \pm 2901	3725 \pm 3105	5778 \pm 4667	6250 \pm 4694		15.2**
Elevation (m)	620 \pm 140	633 \pm 120	654 \pm 173	556 \pm 111	773 \pm 107		33.4***
Slope (degrees)	9.5 \pm 8.5	16.9 \pm 8.6	9.3 \pm 9.5	8.4 \pm 9.1	15.3 \pm 8.2		36.8***
Aspect (degrees)	47	120	68	62	0		
Xylem water potential (MPa)							
Day	-2.38 \pm 0.49 (20.6)	-3.42 \pm 0.61 (17.8)	-2.47 \pm 0.56 (22.7)	-2.09 \pm 0.49 (23.4)	-3.46 \pm 0.36 (10.4)		122.6***
Predawn	-0.72 \pm 0.30 (41.7)	-1.53 \pm 0.56 (36.6)	-1.84 \pm 0.64 (34.8)	-1.22 \pm 0.58 (47.5)	-1.53 \pm 0.42 (27.4)		110.9***
Recovery	1.66 \pm 0.55 (33.1)	1.89 \pm 0.63 (33.3)	0.64 \pm 0.49 (76.6)	0.87 \pm 0.36 (41.4)	1.93 \pm 0.52 (26.9)		115.3***

coastal sage brush, riparian, mixed evergreen forest and oak woodlands. Tree density varies greatly, from open grasslands and savannas with only occasional scattered individuals to mixed hardwood forests with nearly closed canopies (White 1966a, b; Griffin 1971).

Study species. We studied 5 species, all common in the study site (summary information on the taxonomic status of the species is presented in Table 1). Except where noted, distributional information is from Griffin and Critchfield (1972), Munz and Keck (1968), and Hickman (1993).

(1) *Quercus lobata* Nee—The valley oak is a winter-deciduous species, endemic to California, and occurs mostly in valleys, fertile alluvial terraces, on gentle slopes in foothill woodland and riparian forests from 600 m to 1700 m. It is consistently reported as having a deep root system connected to ground water (Griffin 1973).

(2) *Quercus douglasii* Hook. & Arn.—The blue oak is one of the more xerophytic of California oaks (Cooper 1922) and its growth, measured as basal area increment, is reported to have a high correlation with precipitation (Kertis et al. 1993). It is another winter-deciduous species endemic to and widely distributed in California, dominating part of the foothill woodlands on dry, rocky slopes below 1200 m (Baker et al. 1981). This species has previously been found to vary considerably in the degree to which individuals are rooted to the water table (Callaway et al. 1991).

(3) *Quercus chrysolepis* Liebm.—The canyon live oak is an evergreen species and is the most widely distributed oak in California, with a range from Oregon in the north to Baja California in the south. It is common on steep, rocky canyon slopes from 200 m to 2600 m.

(4) *Quercus agrifolia* Nee—The coast live oak is an evergreen species occurring commonly in valleys and on relative wet slopes in both foothill woodland and in mixed evergreen woodland below 1000 m in the northern part of its distribution and up to 1500 m in the southern part. In contrast to the other four species studied here, it is widely distributed along the coast. Canon (1914a, b) reported that this species has an extensive shallow root system. More recently, Griffin (1973) showed that some *Q. agrifolia* are connected to the ground water table.

(5) *Quercus kelloggii* Newb.—The California black oak is a winter deciduous species widely distributed in upland and montane areas mostly from 300 to 2500 m. Little information on the rooting habit has been reported for this species; it is thought to have a single major tap root or numerous major vertical roots (Rundel 1979).

Methods. We measured daytime (DAY) and night-time predawn (PREDAWN) xylem water potential of 87 *Q. lobata*, 56 *Q. douglasii*,

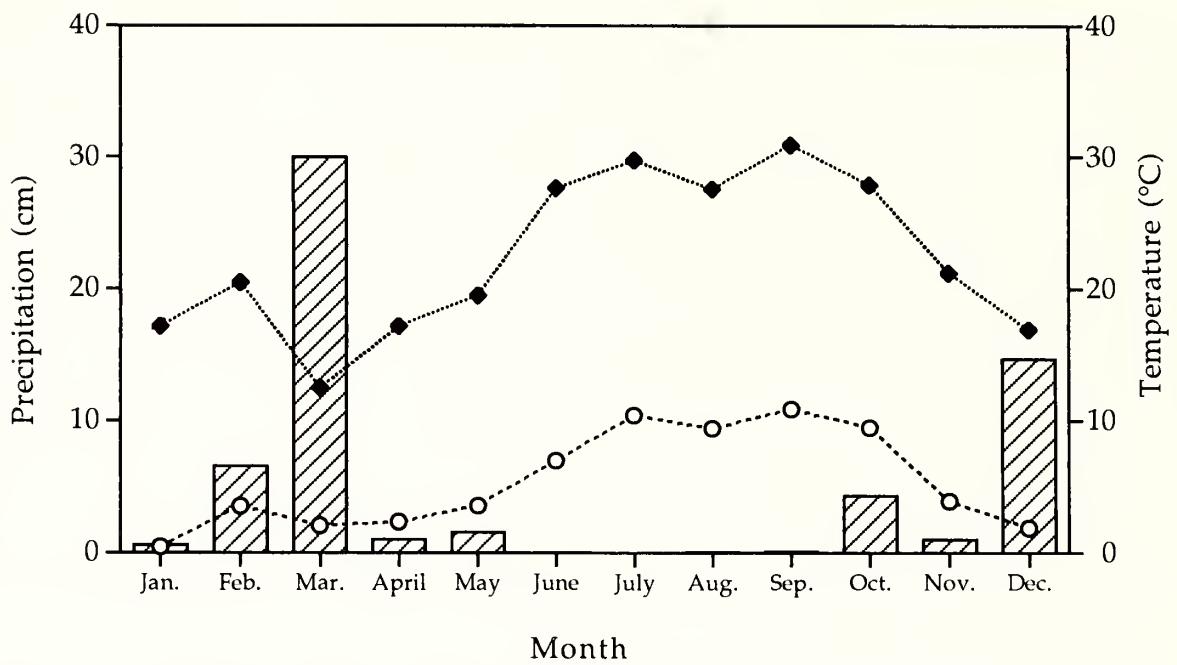


FIG. 1. Precipitation (▨), average monthly maximum (◆) and minimum temperature (○) at Hastings Natural History Reservation during 1991.

63 *Q. agrifolia*, 20 *Q. kelloggii* and 21 *Q. chrysolepis*. Trees were distributed throughout Hastings Reservation over a distance of approximately 3.5 km and were initially chosen in 1980 as part of an ongoing study of acorn production (Koenig et al. 1994). Trees selected were generally large, mature individuals.

Xylem water potential (Ψ) was measured using the pressure chamber technique (Waring and Cleary 1967; Ritchie and Hinckley 1975). Trees were measured with a pressure bomb (PMS Instrument Co.) from 20 September to 5 October 1991. Daytime measurements were made between 1300 and 1700 while nighttime measurements on the same trees were made on the subsequent night between 0200 and 0600. Short shoots, approximately 5–10 cm long with a minimum of 3 leaves were cut from which xylem water potential was immediately measured in the field. We measured 2 shoots per tree; if the difference between them was more than 10%, we measured a third twig. All daytime twigs were cut from branches located in full sunlight.

The study was conducted at the end of the dry season when temperatures are hottest and water stress the greatest (Fig. 1). Furthermore, 1991 followed 5 years of below average rainfall (1 July–30 June seasonal rainfall ranged from 265 mm to 471 mm from 1986–1987 to 1990–1991, 69 to 275 mm below average). Thus, although only a single set of measurements was made on each tree, the values are likely to represent maximum water stress for individuals in this sample.

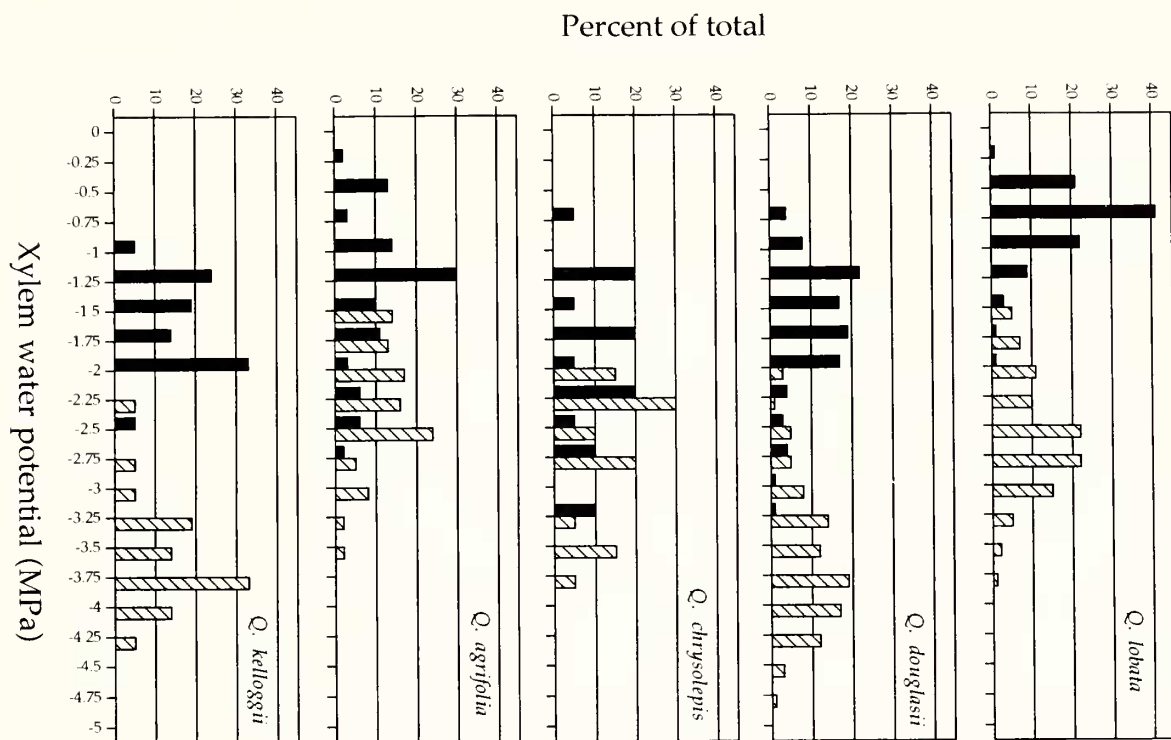


FIG. 2. Predawn and midday xylem water potential (in MPa). ■ predawn values; ▨ daytime values.

RESULTS

Characteristics of trees. The number of stems, the mean size measured of the biggest stem (DBH), the basal area of all stems and elevation of the sampled trees are listed in Table 1. The three deciduous oak species have, in general, one main stem, whereas *Q. agrifolia* and *Q. chrysolepis* have often more than one main stem. Overlap in both size and elevation was extensive for all of the species, as we used similar criteria to initially choose them and we sampled each over the same elevational gradient. However, on average, *Q. douglasii* and *Q. chrysolepis* individuals were smallest and *Q. agrifolia* located at the lowest elevation. *Quercus douglasii* and *Q. kelloggii* individuals tended to be found on steeper slopes than the other three species (Table 1).

Species differed highly significantly from one another in all three measures of xylem water potential (Table 1, Figs. 2, 3). *Quercus kelloggii* and *Q. douglasii* were almost identical with the lowest DAY and the highest RECOVERY values. Mean DAY values were roughly equivalent for the other 3 species, which instead differed greatly in both their PREDAWN and RECOVERY values, with the live oaks (*Q. chrysolepis* and *Q. agrifolia*) having low PREDAWN and low RECOVERY and *Q. lobata* having high PREDAWN and high RECOVERY. The coefficient of variation of the PREDAWN values

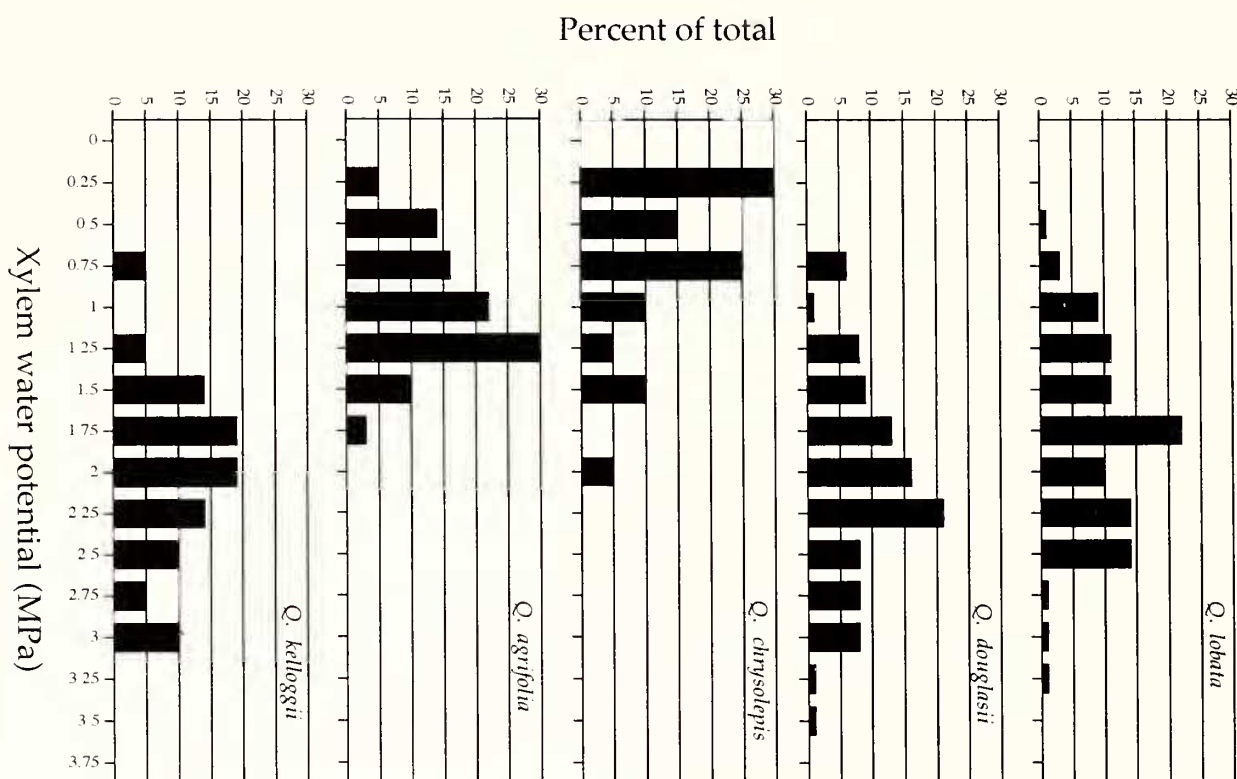


FIG. 3. Recovery of xylem water potential (predawn minus midday values, in MPa).

was twice that of the DAY values, indicating that individuals within each species differ more in their access to water than in tolerance for dehydration. The distributions of Ψ values were not significantly different from normal (15 Kolmogorov-Smirnov 1-sample tests [3 per species], all $P > 0.05$).

Intraspecific correlations of xylem water potential. Table 2 lists Spearman rank correlations of Ψ values with themselves (DAY with PREDAWN) and with DBH, basal area and 2 site characteristics (elevation and slope). Correlations were diverse across the 5 species for all variables. For example, DAY and PREDAWN values were significantly correlated in *Q. douglasii*, *Q. chrysolepis*, and *Q. agrifolia*, but not for either *Q. lobata* or *Q. kelloggii*; elevation and PREDAWN values were positively correlated in *Q. agrifolia* but inversely correlated in *Q. lobata*.

Aspect was tested by comparing mean Ψ values for trees with north, east, south, and west aspects using a Kruskal-Wallis 1-way ANOVA. No significant correlations between aspect and Ψ were found for *Q. agrifolia*, *Q. chrysolepis*, or *Q. kelloggii*. Values for *Q. lobata* and *Q. douglasii* are presented in Table 3. Values were significantly different for PREDAWN (both species) and DAY (*Q. douglasii* only), but differences were not readily interpretable. For *Q. lobata*, north-facing trees had the lowest night values, while for *Q. douglasii*, west-facing trees had the lowest DAY and PREDAWN

TABLE 2. SPEARMAN RANK CORRELATIONS BETWEEN XYLEM WATER POTENTIAL AND TREE/SITE CHARACTERISTICS. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$ (2-tailed).

	<i>Q. lobata</i>	<i>Q. douglasii</i>	<i>Q. chrysolepis</i>	<i>Q. agrifolia</i>	<i>Q. kelloggi</i>
DAY with PREDAWN	0.05	0.42**	0.69***	0.76***	0.05
DAY with					
DBH	-0.04	-0.07	0.40	0.40**	0.15
Basal area	-0.02	-0.07	0.41	0.30*	0.15
Elevation	-0.19	-0.44***	0.64**	0.28*	0.13
Slope	0.06	0.06	0.43	-0.04	0.45*
PREDAWN with					
DBH	0.05	0.06	0.28	0.43***	0.15
Basal area	0.03	0.08	0.29	0.40**	0.15
Elevation	-0.50***	0.13	0.43	0.34**	0.22
Slope	-0.46***	-0.35**	0.42	0.04	-0.33
RECOVERY with					
DBH	0.10	0.09	0.06	0.16	0.09
Basal area	0.08	0.11	0.01	0.28*	0.09
Elevation	-0.07	0.47***	-0.19	0.15	-0.11
Slope	-0.22*	-0.32*	0.06	0.16	-0.64**

values. There were no significant differences in RECOVERY among trees with different aspect.

DISCUSSION

Intraspecific variation. Correlations between site characteristics (elevation, slope, and aspect) and Ψ values were variable and, as previously noted by Griffin (1973), not generally correlated with moisture gradients as they are usually envisioned. For example, water stress should increase with slope, because the redistribution of rainwater through run-off and soil water by saturated throughflow depends on the slope inclination (Band et al. 1993). As expected

TABLE 3. EFFECT OF ASPECT (DIVIDED INTO CARDINAL DIRECTIONS) ON XYLEM WATER POTENTIAL OF *Q. LOBATA* AND *Q. DOUGLASII*. Statistical tests are by Kruskal-Wallis 1-way ANOVA; * = $P < 0.05$.

	<i>Q. lobata</i>				<i>Q. douglasii</i>			
	Day	Night	Recovery	n	Day	Night	Recovery	n
North	-2.41	-1.00	1.41	16	-3.68	-1.45	2.23	5
East	-2.45	-0.79	1.66	23	-3.43	-1.60	1.83	27
South	-2.54	-0.64	1.89	6	-3.13	-1.10	2.02	12
West	-2.28	-0.70	1.58	15	-3.74	-1.77	1.97	10
χ^2 (df = 3)	1.4	8.9*	4.1	—	8.1*	10.8*	1.8	—

from this assumption, the three deciduous species (*Q. lobata*, *Q. douglasii*, and *Q. kelloggii*) all had lower PREDAWN and RECOVERY values with increasing slope (Table 2). However, relationships between slope and both PREDAWN and RECOVERY were positive and nonsignificant for the two evergreen species. We would also predict water stress to be greatest for trees on slopes with a south-facing aspect. In general, there was either no significant relationship between Ψ values and aspect or the relationship did not follow this a priori prediction: for neither *Q. lobata* or *Q. douglasii* were the lowest PREDAWN or RECOVERY values found in individuals on south-facing slopes (Table 3).

Griffin (1973) also found evidence of size-class effects, with smaller trees showing lower Ψ values than larger trees. Our results provide at best weak support for this relationship: DBH or basal area were positively and significantly correlated with DAY, PREDAWN and RECOVERY values for only 1 of the species (*Q. agrifolia*). However, in general we used mature trees; size-class effects may be stronger among younger age classes.

Previously, Callaway et al. (1991) divided *Q. douglasii* at Hastings Reservation into "positive" and "negative" trees based on their PREDAWN values and presumed degree of rooting to the water table. Our data indicate that this categorization is incomplete. The distribution of *Q. douglasii* Ψ values was normally distributed, suggesting that there is a continuum in xylem water potentials for individuals of this species. Also, individual variation in Ψ values among *Q. douglasii* were comparable to that observed within the other four species.

Interspecific variation. Water relations of the five species were distinctly different. *Quercus kelloggii* and *Q. douglasii* demonstrated the greatest drought tolerance as indicated by low DAY and high RECOVERY values (Table 1, Figs. 2, 3). These species were also found on the steepest slopes. *Quercus lobata* showed the highest PREDAWN values probably caused by the use of deep-seated ground water, while *Q. chrysolepis* had the lowest PREDAWN xylem water potential. Species exhibiting the greatest degree of drought evasion as indicated by low RECOVERY values were the live oaks *Q. chrysolepis* and *Q. agrifolia*.

Based on these results the five species can be divided among the categories for coping with dry conditions listed in the introduction (Table 4). *Quercus lobata* exhibits drought avoidance by tapping into and using deep-seated ground water. *Quercus douglasii* and *Q. kelloggii* are the most drought tolerant as indicated by their relatively low DAY values (Scholander et al. 1965; Waring and Schlesinger 1985). The evergreen species, *Q. chrysolepis* and *Q. agrifolia*, are not particularly drought tolerant as expressed by relatively high DAY

TABLE 4. DROUGHT ADAPTATIONS OF CENTRAL COASTAL CALIFORNIA OAK SPECIES INFERRED FROM XYLEM WATER POTENTIAL PATTERNS.

	Elevation	
	Low	High
Drought avoidance	<i>Q. lobata</i>	<i>Q. lobata</i>
Drought tolerance	<i>Q. douglasii</i>	<i>Q. kelloggii</i>
Drought evading	<i>Q. agrifolia</i>	<i>Q. chrysolepis</i>

values and do not appear to tap the ground water to a large extent; growth by these species is limited during the extensive dry season. Instead, these species are drought evasive, shifting part of their growth cycle into the colder part of the year.

Water relations and oak distribution. As noted by prior workers, *Q. lobata* consistently taps the ground water on alluvial terraces where the water table is too low for *Q. agrifolia* to reach. The drought evading *Quercus agrifolia* is better able to grow in canyons and riparian forests as well as in coastal areas where it exploits relatively mesic areas with longer water availability. In addition, *Q. agrifolia* is more shade tolerant (Cannon 1914a, b; Callaway 1992) and is able to form a dense shade and thus has an advantage in low water and nutrient environments over *Q. lobata* (Cooper 1926; Hollinger 1992). *Quercus chrysolepis* appears to function similarly but at generally higher elevations. *Quercus douglasii* and *Q. kelloggii* are the two most drought tolerant species occupying dry slopes and ridges (Griffin and Critchfield 1972), with soils able to supply enough water in the summer.

Distributional preferences of the species were only partially reflected by the correlations between Ψ values and elevation (Table 2). For example, as expected from the generally lower elevational distribution of *Q. douglasii* and higher distribution of *Q. chrysolepis*, DAY values correlated negatively with elevation in the former species and positively with elevation in the latter. However, there was no correlation between Ψ values and elevation in *Q. kelloggii* despite its preference for higher elevations, and there was a positive relationship between DAY values and elevation for *Q. agrifolia*, even though this species prefers lower elevations and is the only one of the five found at sea level in central coastal California.

Our results confirm that trees employing several contrasting water use strategies can coexist within a site. Sympatric oak species segregate by differences in water use depending primarily on the amount of water available in the summer and secondarily on the timing of the main growing season. These differences in water exploitation and drought adaptations probably have major effects on the distribution

(Terradas and Savé 1992) and coexistence (Hall and McPherson 1980) of oaks on a microgeographical scale and, most likely, on a macrogeographical scale as well, thereby contributing to the mosaic of vegetation types dominated by one or more oak species characterizing much of California.

ACKNOWLEDGMENTS

The manuscript was improved by the comments of J. Griffin, R. Myatt, W. Schlesinger, M. Stromberg, and an anonymous reviewer. Financial support was provided by the University of California's Integrated Hardwoods Range Management Program. Additional support for JMHK came from NSF grant BSR89-07405 to T. Nash. We thank Jim Griffin for the use of his pressure bomb and the Marks for logistic support. Thanks also to Anne Royalty and Janis Dickinson for putting up with the authors during the 2 weeks that they were zombified in the midnight pursuit of the data collected for this paper. This paper is dedicated to Jim Griffin in honor of his groundbreaking work on California oaks and his many years of dedication to Hastings Reservation.

LITERATURE CITED

- BAKER, G. A., P. W. RUNDEL, and D. J. PARSONS. 1981. Ecological relationships of *Quercus douglasii* Fagaceae in the foothill zone of Sequoia National Park, California. *Madroño* 28:1-12.
- BAND, L. E., P. PATTERSON, R. NEMANI, and S. W. RUNNING. 1993. Forest ecosystem processes at the watershed scale: incorporating hillslope hydrology. *Agricultural and Forest Meteorology* 63:93-126.
- CALLAWAY, R. M. 1992. Morphological and physiological responses of three California oak species to shade. *International Journal of Plant Sciences* 153:434-441.
- , N. M. NADKARNI, and B. E. MAHALL. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* 72:1484-1499.
- CANON, W. A. 1914a. Specialization in vegetation and in environment in California. *Plant World* 17:223-237.
- . 1914b. Tree distribution in central California. *Popular Science Monthly* 85:417-424.
- COOPER, W. S. 1922. The broad-sclerophyll vegetation of California. Carnegie Institution of Washington, Washington, D.C.
- . 1926. Vegetational development upon alluvial fans in the vicinity of Palo Alto, California. *Ecology* 7:1-30.
- FARQUHAR, G. D. and T. D. SHARKEY. 1982. Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology* 33:317-345.
- GRIFFIN, J. R. 1971. Oak regeneration in the upper Carmel Valley, California. *Ecology* 52:862-868.
- . 1973. Xylem sap tension in three woodland oaks in central California. *Ecology* 54:152-159.
- . 1977. Oak woodland. Pp. 383-416 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. John Wiley & Sons, New York.
- and W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. USDA Forest Service Research Paper PSW-82.
- HALL, S. L. and J. K. MCPHERSON. 1980. Geographic distribution of two species of oaks in Oklahoma in relation to seasonal water potential and transpiration rates. *Southwestern Naturalist* 25:283-295.
- HANES, T. L. 1965. Ecological studies on two closely related chaparral shrubs in southern California. *Ecological Monographs* 35:213-235.

- HICKMAN, J. C. (ed.). 1993. The Jepson manual. University of California Press, Berkeley.
- HOLLINGER, D. Y. 1992. Leaf and simulated whole-canopy photosynthesis in two co-occurring tree species. *Ecology* 73:1–14.
- KERTIS, J. A., R. GROSS, D. L. PETERSON, M. J. ARBAUGH, R. B. STANDIFORD, and D. D. McCREARY. 1993. Growth trends of blue oak (*Quercus douglasii*) in California. *Canadian Journal of Forest Research* 23:1720–1724.
- KOENIG, W. D., R. L. MUMME, W. J. CARMEN, and M. T. STANBACK. 1994. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99–109.
- LARCHER, W. 1980. *Physiological plant ecology*. 2nd ed. Springer-Verlag, Berlin.
- MUNZ, P. A. and D. D. KECK. 1968. *A California flora and supplement*. University of California Press, Berkeley.
- RITCHIE, G. A. and T. M. HINCKLEY. 1975. The pressure chamber as an instrument for ecological research. *Advances in Ecological Research* 9:165–254.
- RUNDEL, P. W. 1979. Adaptations of Mediterranean-climate oaks to environmental stress. Pp. 43–54 in T. R. Plumb (technical coordinator), *Proceedings of the symposium on the ecology, management and utilization of California Oaks*. USDA Gen. Tech. Rep. PSW-44.
- SAWYER, J. O., D. A. THORNBURGH, and J. R. GRIFFIN. 1977. Mixed evergreen forest. Pp. 359–381 in M. G. Barbour and J. Major (eds.), *Terrestrial vegetation of California*. John Wiley & Sons, New York.
- SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, and E. A. HEMMINGSON. 1965. Sap pressure in vascular plants. *Science* 148:339–346.
- TERRADAS, J. and R. SAVÉ. 1992. The influence of summer and winter stress and water relationships on the distribution of *Quercus ilex* L. *Vegetatio* 99–100:137–145.
- WARING, R. H. and B. D. CLEARY. 1967. Plant moisture stress: evaluation by pressure bomb. *Science* 155:1248–1254.
- , J. J. ROGERS, and W. T. SWANK. 1981. Water relations and hydrologic cycles. Pp. 205–264 in D. E. Reichle (ed.), *Dynamic properties of ecosystems*. Cambridge University Press, London.
- and W. H. SCHLESINGER. 1985. *Forest ecosystems. Concepts and management*. Academic Press, Inc., San Diego.
- WHITE, K. L. 1966a. Structure and composition of foothill woodland in central California. *Ecology* 47:229–237.
- . 1966b. Old field succession on Hastings Reservation, California. *Ecology* 47:865–868.

(Received 11 Jan 1994; accepted 19 May 1994)